AMERICAN
JOURNAL OF BOTANY

VOL. VI | MAY, 1919 | NO. 5

OSMOTIC PRESSURES IN THE POTATO PLANT AT VARIOUS STAGES OF GROWTH

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The study of concentration of cell sap in plants has followed, in general, two paths: (1) the relation of the osmotic strength to the physical environment of the plant, and (2) the part which the varying pressures in the roots, stems, and leaves play in the rise of sap.

Since the publication of the paper by Drabble and Drabble (7) on the relation of the osmotic strength of cell sap in plants to their surrounding conditions, other authors have studied the same problem, especially under the extremes to which desert vegetation is subject, since it is in desert plants that the pressure is at a maximum.

The other phase of this study has dealt with the relation of osmotic pressure to sap flow. Dixon (4, 5, 6), either alone or in collaboration with other investigators, has made the most extensive contributions to the solution of this side of the problem, although the work of Hanning (9) should also be mentioned. Dixon and Atkins' (5) observations are so closely related to those made in this paper that they require more than a passing mention.

The osmotic pressure should be higher in the leaves at the top of a tree than in those at its base, if Dixon's theory of the upward pull in the columns of sap in the water-conducting tissue is correct. His observations in general confirm this hypothesis, although there are occasional discrepancies due, as he believes, to the resistance in the conducting tracts. One of his most consistent series of observations, secured with *Wistaria sinensis* leaves, furnishes the following data:

Shaded leaves from 3 feet level,	0.412° depression,	4.95	atmospheres
Exposed leaves from 3 feet level,	0.437° "	5.25	"
Exposed leaves from 27 feet level,	0.550° "	6.61	"

Similar records secured with *Ulmus campestris* show:

Leaves from short shoots at 18 feet level,	0.888° depression,	10.68	atmospheres
Leaves from short shoots at 1 foot level,	0.763 "	9.18	"
Leaves from short shoots at outer end of arched branch in shade at 10 feet level,	1.030° "	12.39	"
Leaves from short shoots on trunk in sunny position at 10 feet level,	1.550° "	18.64	"

[The **Journal** for April (**6**: 131–180) was issued May 1, 1919.]

The first two observations on leaves of Ulmus are comparable since the leaves were situated under similar conditions; the last two records were obtained from leaves from the outside of the crown of the tree in one case and from a very sunny position in the last instance. Shade seems to lower the osmotic pressure even more than a location at the extreme tip of the tree increases it.

The effect of shade on the osmotic strength of the cell sap was even more clearly brought out by a series of observations on the leaves of *Syringa vulgaris:*

Covered 6 days,	1.263°	depression,	15.20 atmospheres
Exposed 6 days,	1.470°	"	17.68 "
Covered 12 days,	1.010°	"	12.15 "
Exposed 12 days,	1.608°	"	19.34 "
Covered 21 days,	.963°	"	11.58 "
Exposed 21 days,	1.505°	"	18.10 "

Dixon says, regarding other observations on the sap from the roots as compared to that of the leaves: "In Syringa the pressure of the sap of exposed leaves was found to vary from 14 to 24 atmospheres, while that of the roots lay between 4 and 6 atmospheres. In Eucalyptus the osmotic pressure of the leaves ranged between 6.1 and 8.4 atmospheres; that of the roots was 5.3 atmospheres."

The effect of wilting on the leaves of *Syringa vulgaris* is as follows:

Control,	1.352°	depression,	16.26 atmospheres
Exposed to light without water supply for 4 hours,	2.002°	"	24.07 "
Exposed to light with water supply for four hours,	1.586°	"	19.08 "

Dixon states as one of his conclusions that: "Other things being equal, mature leaves showed a higher osmotic pressure than developing leaves." No detailed study could have been made at this time as the observations were confined to the months of September and October and the latter part of August.

Dixon and Atkins (6), at a later time, observed the osmotic pressure in the leaves of *Syringa vulgaris* throughout an entire growing season and found that the rise was constant after April but that a rapid decline occurred a few weeks before the leaves dropped from the stem.

In his book on "Transpiration and ascent of sap" Dixon (4) in a footnote says: "In almost every case it was found that the older leaves, *caeteris paribus*, had a higher osmotic pressure on the same plant. This was observed in *Syringa vulgaris*, *Vitis Veitchi*, *Eucalyptus globulus*, *Hedera helix*, and especially in *Ilex aquifolium*. The leaves of the last named evergreen persist through four or five periods of growth, and it is generally found at any time that the osmotic pressure of the sap of the leaves of each successive growth is lower than that of those which precede it."

Hanning's observations (9) on the differences between the osmotic

pressure of the root sap and that from the leaves should be noted. His results were obtained by the plasmolytic method and are of value as a check on those of Dixon, who made only cryoscopic determinations. His trials were made with a long series of plants from all sorts of habitats. The pressure of the root sap in nearly all cases was found to be materially less than that of the leaves. In only 14 percent of the cases did the pressure of the sap from the roots even approximate that from the leaves, while in 51 percent the pressure of the leaf sap, as compared to that of the roots, was in the proportion of 1 : 1.25; in 12 per cent it was in the proportion of 1 : 1.5; and in 23 percent it was even greater, up to 1 : 2.

The potato plant seems thus far to have escaped attention. The only accounts of its osmotic pressures are furnished by Atkins (1), who found the depression in different tubers to range from .538 to .612 degrees, corresponding to 6.47 to 7.36 atmospheres, and by Brannon (2), who found that the sap from tubers kept in an ice box from October 31 to January 23 showed a pressure of 14.51 atmospheres while the sap from tubers kept at room temperature from October 31 to December 5 measured 7.4 atmospheres.

No detailed account seems to have been given, as yet, of the osmotic relations of any herbaceous plant throughout an entire growing season. The potato seems particularly adapted to such investigation because of its succulent leaves and stems. Furthermore, the evolution from tuber to sprout and then to foliage must involve osmotic changes, and it seemed entirely possible that the deposition of starch in the tubers and the tip-burn on the foliage may be related to pressure variations in the leaf or stalk cells.

The yearly recurrence of the physiological disease known as tip-burn was the immediate stimulus to the undertaking of this study. Even during ordinary seasons, between a third and a half of the foliage in the Vermont fields is destroyed during the latter part of July and the month of August by the intense sunlight and heat. The older plants are then affected, the younger ones escaping until they attain a certain stage of maturity, when they, too, succumb.

The formation of tubers and flowering seem to mark a sharp crisis in the life of the plant. Attention was directed by this point by Jones (11) in 1903, who said that: "Reproduction by seeds is a sexual process, that by tubers is vegetative. Both are exhaustive of vital forces. The two are, therefore, in a physiological sense opposed and cannot well be carried on at the same time. Under the natural condition of the wild plant the seed precedes; with our shorter season and intensive culture we have crowded the two processes together until they tend to overlap. That is, we have forced the tuber production back into the period which in the wild plant is given to the production of flowers and seeds. As a result, we have, just after the potato plant comes into blossom, a strained and unnatural condition; a state of physiological tension, of stress between two opposing vital tendencies. According to the mode of its ancestors the major part of the

plant's energy would then be tending upward toward flower and seed; but tuber production in the high-bred specialized plant begins immediately, and the acquired tendency is for this process to claim the major part of the food.

"As a result of this conflict of tendencies in the plant there occurs a *critical period* during which the continued health of the plant, if not its very life, hangs in the balance.

"Whether this explanation is correct or not, the fact is certain that the fortnight including and immediately following the blossoming period is the turning point, the crisis in the life of the potato plant."

The soil of the region around Burlington, Vermont, is in the main a light sandy loam. On this soil tip-burn, which is the external evidence of the crisis through which the plant passes, is severe. No better location, therefore, could be found for making observations on the internal factors, chemical and physical, that are at play inside the potato plant during the growing season. However, the crisis mentioned by Jones is more than a fortnight long; it lasts at least a month or six weeks, as the observations made during the course of the present work will show.

The osmotic pressures in the plant are the result of the presence of sugars or inorganic salts in solution in the cell sap. So far as could be ascertained no analysis of the sap itself was available, but the ash of the plant has been investigated a number of times.

Choslowski (3) found considerable percentages of glucoses early in the season both in the pith and in the vascular portions of the potato stalk. After June 28 only the pith contained glucoses. After August 26, two weeks before the death of the plants, the percentage of sugars in the stems had diminished. The young tubers and their stolons were very rich in glucose early in the season, but after June 28 showed little sugar. He attempts no explanation as to their movement other than to state that they move in a diosmotic manner.

Kellermann (12) determined that the calcium, potassium, and phosphorus in the ash of potato leaves and stalks increased to a certain maximum during the summer and then rapidly fell away during the last few weeks of growth.

Seissl and Gross (15, 16) found that the potato leaf ash contained a maximum of P_2O_5 and K_2O on July 1 and that the percentages decreased from that date until the harvest, October 10. The same investigators also found generally a maximum percentage of CaO, MgO, K_2O, SO_3, and P_2O_5 in the leaf ash on either July 1 or August 1, with a decrease after the latter date. A few exceptions to this rule can be found in their tables of analyses, but these are due to specific fertilizer applications. The late summer and autumnal decreases in CaO, MgO, SO_3, and P_2O_5 percentages were especially marked with the Johannis, while the decrease in P_2O_5 content was notable in both Johannis and Perkun, whatever the fertilization.

Methods

The plants were brought in from the field or garden during the summer of 1918, and the sap was immediately extracted from the leaves, stems, or tubers by grinding up these organs in a small Excelsior food chopper and pressing the juice through cheesecloth. The requisite 12–15 c.c. needed were usually easily obtained as all the organs except the roots are very succulent. The sediment was allowed to settle and the upper portion decanted off. The freezing was done with the help of an ordinary Beckmann thermometer and apparatus. At least two determinations were made in each case, and if no super-cooling appeared, the trials were repeated three or more times. It was impossible to obtain any super-cooling with a few samples of leaf juice, but enough attempts were made so that the true freezing point was closely approximated. Correction of the depressions was made for super-cooling using the formula suggested by Harris and Gortner (10), and their tables have been employed in converting the depressions in degrees into atmospheres. In a number of cases, the juice was analyzed for glucoses (or reducing sugars) and sucrose by the gravimetric Fehling's method. The presence of various organic materials in the juices introduced disturbing factors, but the determinations at least afford some idea of sugar percentages. Complete analyses were made of four juices. The author acknowledges the help of Mr. R. L. Gale, who had general charge of the analytical work and who assisted with the cryoscopic readings.

Green Mountain potatoes were used in all cases unless otherwise stated.

Comments on Observations

The freezing point of the tuber sap varied considerably, as might be expected in view of the conditions under which the tubers were kept. However, in every case the pressure exceeded 7 atmospheres. These depressions were greater than those obtained by Atkins (1) but correspond very closely to those secured by Brannon (2) for other varieties of potatoes kept at room temperatures. The pressure in the sprouts was even more variable, covering a range of from 6 to 12 atmospheres. The sprouts used in reading no. 3 (table 1) were obtained from the tubers used in reading no. 2. It will be seen that the pressure in the sprouts was 8.75 atmospheres while that in the tubers was 7.691 atmospheres. The sugars were more than twice as abundant in the sprouts as in the tubers and were the cause of the increased osmotic pressure.

The osmotic pressure of the sap of the very young plants was not determined during June and early July. The first records were secured on July 18 when the plants were full grown, in bloom, and with tubers a centimeter or a centimeter and a half in diameter. No tip-burn had appeared as yet, and the plants were turgid and healthy. The results secured on this particular plant indicate the greatest pressure in the stalks. The weather

TABLE I

No.	Date (1918)	Weather	Material	Depression	Depression in Atm.	Percent Glucose	Percent Sucrose	Remarks
1	June 9		Green Mt. tubers kept in dry room.	.856	10.30	.497	.769	
2	July 5		Green Mt. tubers from greenhouse cellar.	.639	7.69	.946	.950	
3	" 5		Sprouts from above.	.727	8.75	2.32	2.25	
4	June 14		Sprouts from tubers in barrel.	.985	11.86			
5	" 17		Sprouts from tubers in boxes.	.876	10.55			
6	" 17		Long, slender sprouts.	.510	6.14			
7	8 A.M. July 18	A bit cloudy. Rain on July 17.	New leaves.	.434	5.23	6.16	Undet.	No tip-burn.
8	"		Old leaves.	.523	6.30			
9	"		Stalks.	.626	7.54			
10	"		Tubers.	.453	5.46	.508	.899	
11	4 P.M. July 20	Clear. Two preceding days hot and clear.	New leaves.	.670	8.07	.484	.881	No tip-burn.
12	"		Old leaves.	.653	7.84	.185	.208	
13	"		Stalks.	.670	8.07	.228	1.115	
14	"		Tubers.	.506	6.10	.299	.873	
15	8 A.M. July 22	Hot, cloudy. Warm and clear on preceding day.	New leaves.	.567	6.83	.000	trace	Tip-burn begins.
16	"		Old leaves.	.604	7.28	.207	.067	
17	"		Stalks.	.622	7.49	.171	.278	
18	"		Tubers.	.492	5.93	.000	.306	
19	July 23	Slightly hazy, but hot with high humidity.	New leaves.	.691	8.32	1.333	.090	Tip-burn shows from preceding day.
20	"		Old leaves.	.631	7.60	.909	.324	
21	"		Stalks.	.720	8.67	1.429	.000	
22	"		Tubers.	.527	6.35	.444	1.161	
23	5 P.M. July 25	Previous day warm and with sunshine.	New leaves.	.536	6.46	1.020	.000	Continued tip-burn.
24	"		Old leaves.	.568	6.84	1.068	.000	

TABLE 1 (*Continued*)

No.	Date (1918)	Weather	Material	Depression	Depression in Atm.	Percent Glucose	Percent Sucrose	Remarks
25	5 P.M. July 25		Stalks.	.703	8.47	1.016	.021	
26	"		Tubers.	.412	4.96	.588	.706	
27	10.45 P.M. July 25	After a bright, hot day.	New leaves.	.640	7.71	.1714	Undet.	
28	"		Old leaves.	.602	7.25	.000	.000	
29	"		Stalks.	.781	9.41	.186	2.146	
30	"		Tubers.	.541	6.52	.000	1.073	
31	9.30 A.M. July 27	Hazy, but hot. Preceding day fair.	1st row of greenhouse plot. New leaves.	.754	9.08			
32	"		Old leaves.	.732	8.82			
33	"		Stalks.	.828	9.97			
34	"		Tubers.	.594	7.16			
35	"		2nd row. New leaves.	.754	9.08			
36	"		Old leaves.	.689	8.30			
37	"		Stalks.	.944	11.37			
38	"		Tubers.	.587	7.07			
39	11 A.M. July 29	Hazy but hot.	New leaves.	.742	8.95	.000	.201	Plants a little wilted from the intense heat of the previous day. Tip-burn advances.
40	"	Previous day hot and dry.	Old leaves.	.710	8.55	.000	.235	
41	"		Stalks.	.886	10.70	.000	.766	
42	"		Tubers.	.533	6.42	.000	.489	
43	10 A.M. July 30	Clear. Heavy rain previous night.	New leaves.	.539	6.49	.009	.755	Plants turgid.
44	"		Old leaves.	.488	5.88	.000	.544	
45	"		Stalks.	.821	9.89	.072	2.270	
46	"		Tubers.	.486	5.86	.000	.000	
47	5 A.M. July 31	Cool, partly cloudy. Cloudy preceding day.	New leaves.	.514	6.19	.019	.023	
48	"		Old leaves.	.522	6.29	.000	.000	

TABLE I (*Continued*)

No.	Date (1918)	Weather	Material	Depression	Depression in Atm.	Percent Glucose	Percent Sucrose	Remarks
49	5 A.M. July 31		Stalks.	.874	10.53	.000	.027	
50	"		Tubers.	.489	5.89	.000	Trace	
51	9 A.M. July 31		Corn leaves.	.569	6.85	.028	.032	
52	"		Corn stalks.	.624	7.52	.017	Trace	
53	"		Bean leaves.	.792	9.54	.009	.000	
54	"		Bean stalks.	.918	10.94	.000	.064	
55	"		Bean pods and beans.	.716	8.62	.045	.000	
56	Aug. 7	Warm and fairly bright.	Leaves of young plant.	.606	7.30	.000	Trace	Flower buds showing and tubers beginning to form.
57	"		Stalks, young plant.	.579	6.98	.000	"	
58	"		Seed piece, plant.	.566	6.82	.000	.752	
59	"		Leaves, old plant.	.749	9.02	.000	.000	With large tubers and flowers almost past.
60	"		Stalks, old plant.	.840	10.12	.006	2.064	
61	2.30 P.M. Aug. 8	Cloudy, warm, and humid. Rain previous night.	Leaves, young plant.	.672	8.08			
62	"		Stalks, " "	.684	8.24			
63	" .		Leaves, old plant.	.754	9.08			
64	"		Stalks, " "	.824	9.92			
65	"		Tubers, " "	.554	6.67			
66	2.30 P.M. Aug. 17	Cold, brilliant sunshine.	Inside of leaflet of young plant.	.868	10.45	.000	.076	
67	"		Periphery of leaflet of young plant.	.925	11.14	.000	1.447	
68	"		Stalks, young plant.	.685	8.25	.000	.000	
69	"		Inside of leaflet, old plant.	.787	.948	.000	.546	
70	"		Periphery of leaflet of old plant.	.836	10.08	.000	1.236	
71	"		Stalks, old plant.	.821	9.89	.000	.000	
72	11 A.M. Aug. 19	Cold, brilliant sunshine.	Sunflower leaves, inside.	1.026	12.35	.383	.939	
73	"		Sunflower leaves, outside.	.940	11.32	.393	.450	
74	4.30 P.M. Aug. 19	" " "	Inside of leaves, old plants.	.877	10.56	.000	.460	

TABLE 1 (*Continued*)

No.	Date (1918)	Weather	Material	Depression	Depression in Atm.	Percent Glucose	Percent Sucrose	Remarks
75	4.30 P.M. Aug. 19		Periphery of leaves, old plants.	.992	11.93	.000	1.054	
76	8.30 A.M. Aug. 20	Cool, brilliant sunshine.	Tips of leaflets, old plants.	.957	11.52	.000	.479	
77	"		Butts, old plants.	.848	10.22	.000	.000	
78	2 P.M. Aug. 22	Clear and warm.	Inside of leaflets, old plants.	.845	10.19			
79	"		Periphery of leaves, old plants.	.992	11.94			
80	9 A.M. Aug. 27	Clear and warm.	Dahlia leaves.	.557	6.71			
81	"		" stalks.	.541	6.52			
82	"		" tubers.	.549	6.61			
83	2 P.M. Aug. 27	Clear and bright.	Young leaves.	.692	8.34			
84	"		Old "	.717	8.63			
85	"		Wilted "	.837	10.08			
86	9.30 A.M. Aug. 28	Clear and bright.	Chicory leaves.	.870	10.48			
87	"		" stalks.	.840	10.12			
88	"		" roots.	.712	8.58			
89	2 P.M. Sept. 1	Cool with brilliant sunshine.	Leaves, old plant	.810	9.75	.000	.067	Plants were about a third dead from tip-burn. Some new growth. For complete analysis, see Table 2.
90	"		Stalks, " "	.746	8.98	.000	.000	
91	"		Tubers, " "	.511	6.16	.000	.000	
92	"		Leaves, young plant.	.580	6.99	.000	.000	
93	"		Stalks, " "	.561	6.76	.000	.000	
94	2 P.M. Sept. 9	Cool with brilliant sunshine.	Leaves, young mosaic plants.	.650	7.83	.660	.000	
95	"		Leaves of plants shaded 48 hours.	.522	6.29	.000	.000	
96	"		Stalks of plants shaded 48 hours.	.538	6.48	.000	.000	

TABLE 1 (*Continued*)

No.	Date (1918)	Weather	Material	Depression	Depression in Atm.	Percent Glucose	Percent Sucrose	Remarks
97	Sept. 18	Cool and cloudy. Cloudy preceding day.	Old (green) stalks	.502	6.05	.000	.000	Still with some green leaves. For complete analysis, see Table 2.
98	"		Old (yellow) stalks.	.354	4.27	.000	.000	
99	11 A.M. Sept. 19	Clear and cool.	Young leaves of old McCormick plants.	.633	7.63			After continued rains.
100	"		Part of upper stalk	.671	8.08			
101	"		" lower "	.660	7.95			
102	"		Roots.	.355	4.28			
103	"		Tubers.	.557	6.71			
104	"		Balls.	.534	6.44			Stalks of fruit dead in some cases.
105	"		Young leaves (wilted).	.885	10.66			
106	"		Upper stem (wilted).	.786	9.46			
107	Sept. 24	Cold. Rain for two weeks.	Leaves, old plant (Green Mt.).	.645	7.77			After long rains with little sunshine.
108	"		Stalks, " "	.616	7.42			
109	"		Tubers, " " (Green Mt.).	.528	6.36			
110	"		Leaves, young plants.	.686	8.26	1.386	.359	Growing since about August 7.
111	"		Stalks, " "	.680	8.19	1.466	.613	
112	"		Seed piece.	.532	6.41	2.610	.172	
113	"		Tubers, young plants.	.589	7.09	.816	1.796	
114	Sept. 24	Rain for two weeks.	Tomato leaves (Yellow Plum).	.633	7.64			
115	"		" stalks.	.647	7.79			
116	"		" green fruit.	.557	6.70			
117	"		" ripe "	.620	7.46			
118	10 A.M. Sept. 28	Cool and cloudy.	Garden beet leaves.	.733	8.83	.000	.000	
119	"		Garden beets.	.981	11.81	.000	5.590	
120	"		Carrot leaves.	.980	11.80			
121	"		Carrots (McCormick).	.812	9.77			
122	"		New leaves.	.658	7.93			Old plants, growing all summer, but recently putting out new foliage.

TABLE 1 (*Continued*)

No.	Date (1918)	Weather	Material	Depression	Depression in Atm.	Percent Glucose	Percent Sucrose	Remarks
123	Sept. 28		Stems.	.598	7.20			
124	"		Tubers.	.566	6.80			
125	5 P.M. Oct. 1	Clear and cool. Rain previous night.	Leaves (normal).	.780	9.39	.202	.384	Plants set out about Aug. 7. Growth had ceased and tubers were being formed.
126	"		Stalks "	.689	8.30	.535	.048	
127	"		Leaves (mosaic).	.831	10.00	.192	1.186	Plants similar to above; leaves dying in spots.
128	"		Stalks "	.631	7.60	.277	.331	
129	"		Sugar beet leaves (outer).	.801	9.65			Outer leaves turning yellow.
130	"		Sugar beet leaves (inner).	.949	11.42			
131	"		Sugar beets.	1.429	17.18	.000	12.626	
132	"		Sugar beet leaves.	1.014	12.21	1.280	.000	
133	"		Ripe tomatoes (Yellow Plum).	.617	7.43			Very ripe fruit.

of the two preceding days had been rainy. Later observations revealed the fact that such atmospheric conditions tend to lower the pressure in the leaves while that in the tubers and stems remains almost constant. The records made two days later are, therefore, to be taken as representing more nearly the relative pressures in the various parts of the plant during average July weather. At that time the pressures had all risen, but particularly that of the leaves. Two hot, clear days had intervened. In the latter case, the stalks displayed a high osmotic pressure but it was not much above that of the leaves. The same observations can be made on the determinations of July 22 when tip-burn began to be noticed on some of the plants.

A period of intense heat and extensive tip-burn injury then ensued. The sap in the leaves and stalks exhibited a much smaller depression when obtained at 5 A.M. on July 25 than that at 5 P. M. on July 23, 10:45 P.M. July 25, 9:30 A.M. July 27, or 11 A.M. July 29. The great preponderance of the pressure in the juice from the stalks is the striking feature of the observations made during this intensely hot week; in one instance this pressure increased to 11.37 atmospheres. The tuber sap pressure seemed to be more stable, although in one case it rose to 7.16 atmospheres. An analysis of the juices revealed a high sugar content in the stalks at all times, 2.146 percent of sucrose on July 25 being the maximum. The osmotic pressure in the tubers must also be largely maintained by sugars, both reducing sugars and sucrose being always present in large amounts.

A heavy rain on the night of July 29 broke the hot spell of weather, and the response of the plants was almost immediate, as the observations made at 10 A.M. on July 30 indicate. The sap in the stalks, with a sucrose content of 2.27 percent, did not change as rapidly, although the pressure was somewhat less than it had been the previous day.

The high pressure in the juice from the stalks was at 5 A.M. July 31, but the pressures in the juices of the leaves and tubers were approximately the same as those obtained at 10 A.M. the preceding day.

The next observation was made on August 7, when the sap from young plants was compared with that from fully grown specimens. The striking fact here presents itself that in the young plants all the organs exhibited nearly the same osmotic pressure and that the leaves take the lead by about a half-atmosphere. The juice from the old seed tuber, as might be expected, produced the smallest depression. The pressure of sap from the stalks of the old plants was almost an atmosphere greater than that from the leaves. The relatively high sucrose percentage in the stalks should be noted.

A repetition of this series of observations was made at 2:30 P.M. August 8. The stalk sap, in this case, recorded a slightly larger depression than the leaf sap, but the difference between the juices of the old leaves and those of the stems amounted to over 0.8 atmosphere.

The trials made on August 17 were meant to determine the osmotic

pressure in the sap of the periphery of the leaflets as compared to that near the midribs. The leaflets were cut as shown in Fig. 1. Both old and young plants were used. Errors were introduced into the determination by the evaporation from the cut surfaces, but the readings were at least comparative. The sap obtained from the periphery of the leaflets from both young and old plants recorded a higher osmotic pressure than the sap secured from the region of the midrib. The high percentage of sucrose in the peripheral portions must also be noted. Similar trials were made on August 19, when even greater preponderances in peripheral osmotic pressures and sucrose contents were evidenced. Similar cryoscopic results were recorded on August 22, although the sugar determinations were not made.

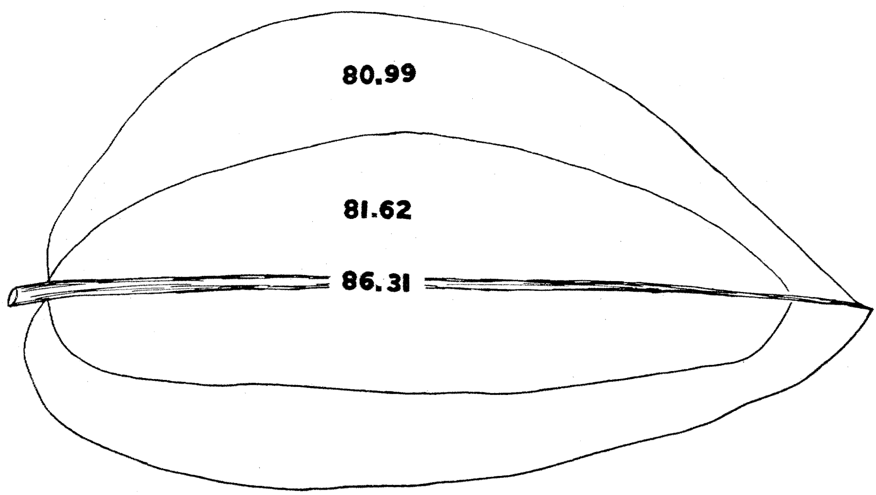

FIG. 1. Potato leaflet, percentage of water in the periphery near the midrib, and in the midrib.

Sunflower leaves were similarly tested on August 19, and showed reverse results both as to pressure and sucrose percentages.

A determination was made on August 20 of the depressions of the saps secured from the tips and from the butts of the leaflets. The tips showed over an atmosphere greater pressure than the butts, due to higher sucrose percentages.

The water content of the leaflets was determined by cutting them up into small pieces as indicated in Fig. 2, weighing, drying at 100° C. for 4 to 5 hours and reweighing. While the leaflet periphery contained sap of a higher osmotic pressure than that in the midrib (2), the leaflet really is much more succulent along the midrib and toward the base than it is toward its outside. The leaflet, in spite of the higher peripheral osmotic pressure,

loses water from these parts at such a high rate on hot days that these portions are often found to be wilted.

A large dahlia plant with almost full grown flower buds, used on August 27, seemed to be at an osmotic equilibrium.

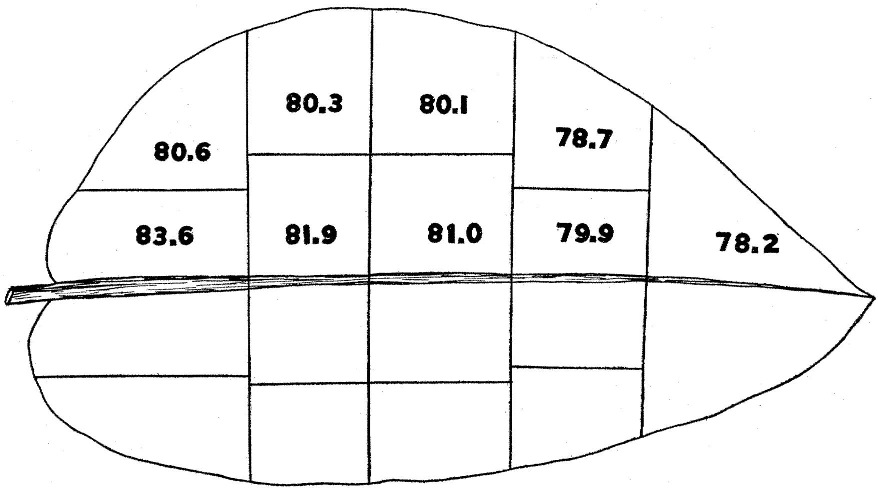

FIG. 2. Potato leaflet, percentage of water in various portions of the lamina.

Chicory plants (August 28) showed an osmotic pressure of almost two atmospheres more in the leaf than in the root sap, with the stalk sap intermediate between the two. Chicory behaved in every way as would be expected if, as a matter of fact, osmotic pressure is the cause of the upward sap flow.

Heavy rains occurred during early September, cool weather followed, and the older potato plants that had not entirely succumbed to tip-burn began to resume growth. Cryoscopic readings were taken on September 9 of the juice from an old plant and from some young plants growing in a parallel row since the first week in August. The striking features at this time were the relative pressures in the leaves and stalks, the pressure in the tubers having remained about constant. The osmotic pressure in the leaf sap had greatly increased, so much so, in fact, that it exceeded that of the stems by 0.77 atmosphere. The young plants corroborated the readings of August 7 and 8, the leaf sap pressure being greater than that of the stalks. The increase in pressure in the old plant seems largely due to the inorganic salts soluble in the cell sap, since the sugars were conspicuously absent at this time. The cooler weather and lack of sunshine were probably responsible for the latter condition. A complete analysis was made of the ash of the sap used in these cryoscopic determinations (table 2).

TABLE 2.

PERCENTAGE OF WATER SOLUBLE SALTS IN JUICES.

Sept. 9, 1918. Old plants.

	P_2O_5	Cl	SO_3	CaO	MgO	Na_2O	K_2O	Total
Leaves	.496	.180	.128	.353	2.260	.133	.120	3.671
Stalks	.558	.192	.139	.378	1.487	.035	.359	3.148
Tubers	.821	.046	.241	.394	1.111	.096	.071	2.761
Sept. 9, 1918. Young plants.								
Leaves	.472	.061	.235	.186	.871	.044	.065	1.935
Stalks	.205	.053	.040	.256	1.013	.073	.075	1.715

The foliage on many of the old plants was largely dead by September 18, but the stalks, together with small tufts of leaves, were still green. Other plants had lost their foliage entirely and their stalks were of a yellow-green hue. The diminution in the osmotic pressure of the sap from these stalks that were still green is marked, but it is even more so in the yellow-green ones. The sugars were entirely absent. Analyses of the ash of the saps appear in table 3.

TABLE 3.

PERCENTAGE OF SALTS IN JUICE OF STALKS

Sept. 18, 1918.

	Old Stalks	Green Stalks
CaO	= .949%	2.212%
SO_3	= .029%	.207%
MgO	= 1.364%	1.815%
Cl	.076%	.142%
P_2O_5	= .552%	.603%
Na_2O	= .089%	.142%
K_2O	= .088%	.130%
	3.141% ash.	5.251% ash.

It will be seen that as the foliage and stalks die and the tubers mature, the latter withdraw from the aerial portions a considerable portion of the soluble materials. These results on the ash of the soluble salts in the sap agree with those secured by Kellerman (12), noted before.

The McCormick plants used on September 19 still showed a slightly higher osmotic pressure in the stalk sap than in the leaf sap, the sap in the upper part of the stalk did not differ materially from that in the lower part, the roots exhibited a remarkably low pressure, while the fruit and tubers occupied in this respect an intermediate position between the leaves and roots. Two of the plants were allowed to transpire in a current of air for five hours, and the freezing points of the juice from the leaves and the upper part of the stalk were again determined. The incipient wilting had raised the osmotic pressure of the leaf sap 3 atmospheres or 39 percent, while in

the stalks the increase was only 1.38 atmospheres or 17 percent. On August 27 a similar experiment had been made on leaves removed from the plant and allowed to transpire for 2½ hours. The increase in this instance was 1.6 atmospheres or about 18 percent.

The young Green Mountain plants, growing since about August 7, had developed tubers a centimeter or more in diameter in about seven weeks. The leaves and stalks exhibited about the same pressure, while that of the tubers was rather higher than usual and that of the seed piece was very low. The large amount of sugar present in all the organs was conspicuous and is comparable to that in the plants, used on July 20, 22, and 23, which were in about the same stage of development. The increase in the osmotic pressure in all parts of the plant, too, shows that the soluble materials at this stage of growth had about reached their maximum.

The only other observations on normal potatoes were made on September 28, on some old McCormick plants that had started to put out new foliage. The new leaves at this date contained a sap with an osmotic pressure 0.73 atmosphere higher than the sap of the stems. On September 19, the reverse had been true.

Shading the potato plant diminishes the osmotic pressure of the sap of the leaves and stalks. The pressure in the leaves of a normal young plant on September 9 was 6.99 atmospheres, while that found in a plant shaded for 48 hours was only 6.29 atmospheres. In the stalks of the same plants, the pressures were 6.76 and 6.48 atmospheres. Shading, therefore, by lowering the osmotic pressure would enable parasitic fungi more readily to obtain their food material and to increase their rate of growth. Dark, cloudy, rainy days would be very effectual to this end, since increased moisture seems to lower the pressure, as is clearly shown by the observations on July 27 and 29 taken before a rain, and on July 30 and 31 after a rain. The relation of lowered osmotic pressure to the spread of epidemics due to fungi has not been heretofore recognized clearly, although Dixon and Atkins (5) have already pointed out that shading had this effect on the leaves of Syringa:

Covered, 2 days,	21.63	atmospheres
Exposed, 2 days,	24.57	"
Covered, 3 days,	19.03	"
Exposed, 3 days,	20.00	"
Covered, 7 days,	15.97	"
Exposed, 7 days,	19.12	"

The effect of the weather was also noted by them on the same plant:

Leaves, gathered after a dark day, no sunshine, 16.26 atmospheres
Leaves, gathered after a bright day, 9 hours' sunshine, 22.40 atmospheres
Leaves, gathered after a bright day, 7 hours' sunshine, 20.40 atmospheres

The checking of epidemics of *Phytophthora infestans* by hot, dry weather is usually ascribed to a "drying up" of the fungus in the leaf. This is

probably literally true. The fungus may be able to withdraw food materials from the leaf when the pressure is only about 6 atmospheres, as on July 31, but when this pressure rises to 9 or 10 atmospheres, as on August 8, the parasite may itself lose all its water and be unable to recover.

Cryoscopic readings of the sap from plants badly affected by mosaic were made on September 9 and on October 1. The leaf sap of the mosaic plant recorded a pressure of 7.83 atmospheres, while that from a normal plant growing near it showed only 6.99 atmospheres. The mosaic leaves also contained an unusually high percentage of reducing sugars. The pressure in the normal leaves on October 1 was 9.39 atmospheres, while in the mosaic leaves it was 10 atmospheres. The much higher percentage of cane sugar should also be noted. On the other hand, the sap of the normal stalks exhibited a pressure of 8.30 atmospheres while that of the mosaic ones showed only 7.60 atmospheres. The higher pressures in the mosaic leaf sap seem to be due to the presence of abnormally large amounts of sugars. This may indicate an inability on the part of organs so affected either to transform or to transport their carbohydrates.

Comparison of the potato plant with nearly related plants, such as the tomato, or with vegetables that deposit their carbohydrates in enlarged roots, such as the carrot or the beet, ought to throw some light on the pressures in storage organs or fruits. The juices from the tomato plant tried on September 24 recorded about the same pressures in leaves and stalk. Growth at this time had ceased. The low osmotic pressure in the green fruit is peculiar but corresponds almost exactly with the pressure in the fruit from the potato on September 19.

The ripening of the tomato fruit increased its osmotic pressure 0.76 atmosphere as shown on September 24 and verified on October 1, with very ripe fruit. Unfortunately no tomato plants were used for osmotic pressure experiments during the very hot weather in August, but the probability is that the stalk sap would have shown a higher pressure than the leaf sap, as was the case with the potato in that period. Corn, on July 31, recorded a pressure of 6.85 atmospheres in the leaves and 7.52 atmospheres in the stalks, while beans gave a pressure of 9.54 atmospheres in the leaves, 10.94 atmospheres in the stalks, and only 8.62 atmospheres in the pods and beans.

Carrots, on September 28, exhibited 11.80 atmospheres pressure in the sap from the leaves and 9.77 atmospheres in the sap from the roots themselves.

Garden beets, on September 28, had 8.83 atmospheres pressure in the leaf sap and 11.81 atmospheres in the beet root sap. The 7.5 percent of cane sugar in the root explains the unusually high pressure. Sugar beets and sugar beet leaves were tried on October 1. The inner leaves were still growing and their sap had a pressure of 11.42 atmospheres while the outer ones gave only 9.65 atmospheres. Another lot of beets recorded 12.21 atmospheres for the leaves and 17.18 atmospheres for the roots. The

latter pressure is developed from the 12.6 percent of cane sugar of the sap, while the 1.28 percent of reducing sugars in the leaves helped to maintain the equilibrium to some extent.

General Discussion

A *résumé* of the observations made on the osmotic pressure of the potato plant at different periods of development seems to show the following conditions to succeed each other:

1. The normal pressure in the seed tubers as they are taken from storage is between 7 and 10.3 atmospheres.
2. The sprouts which come from these tubers, not in the soil, exhibit a pressure slightly in excess of that of the tubers themselves.
3. This pressure for the tubers or seed piece is lowered by the absorption of water until it drops to 6.82 (August 7), or 6.41 atmospheres (September 24).
4. The juice of the leaves of the young plant records a higher osmotic pressure than that of the stalk, and the osmotic pressures of the juices from both leaves and stalk are greater than that of the juice from the old seed piece.
5. The osmotic pressure becomes greater in the stalk than in the leaves after the flower buds are put out and the tubers begin to grow.
6. The growing tubers maintain an almost constant pressure from the time they are of a sufficient size for the determination of pressure until maturity.
7. The pressure in the stalk is less variable than that in the leaves and continues high throughout the active tuber and starch period.
8. The return of cool, rainy weather starts growth of the foliage again, and the osmotic pressure in the leaves again becomes greater than that in the stalks.
9. The osmotic pressure in the old plants is higher than that in the young ones.
10. The pressure diminishes again in the very old plants that have lost practically all their foliage and sinks to a very low ebb in the yellow-green stalks with no foliage.

These observations have a distinct bearing on certain conclusions, both theoretical and practical.

1. A superior osmotic pressure seems to be necessary for the formation of new growth. The sprouts have a greater osmotic pressure than have the tubers from which they arise. The leaves have a higher osmotic pressure than the stalks during the early growth period while the foliage is being produced, but as soon as they lose that predominance, the growth stops and is not resumed until the predominance is again assumed, usually late in the growing season, in September.

2 A superior osmotic pressure is not necessary to maintain an organ after it has been formed. The leaves during July and August do not have as high an osmotic pressure as do the stalks, but they are able to maintain themselves and produce large quantities of starch. It seems necessary to assume, therefore, that the transpiring organs are connected directly with the root system by a long series of tubes in which the cross walls offer a very slight opposition to the hydrostatic head while their side walls are comparatively impermeable. The rapid recovery of an herbaceous plant from wilting would support this theory, as would also the sudden drop in osmotic pressure of the sap from the leaves between 11 A.M. July 29, and 10 A.M. July 30, during which period a heavy rain occurred. The plants on July 29 were in a state of incipient wilting. The water that came to them must have passed through a long zone in the stalk where the osmotic pressure was greater outside the water-conducting tubes than it was inside them; still, these leaves did not wilt to any great extent. The question of the maintenance of turgor in the leaves of plants like the beet seems to have been overlooked by Dixon (4) in his theoretical discussions of sap flow, a though the conception he presents (pp. 141–142) of transpiring leaf cells at the upper end of a long tube (the tracheae) is the correct one. The osmotic pressure in these leaf cells is a measure of the pressure in the tracheae and in the conducting tissue, but not necessarily of that in the tissues in which the water tubes are imbedded. It would seem, therefore, that to the conception of transpiring cells at the upper end of a series of tubes should be added the idea of a direct connection of these tubes with the absorbing cells of the roots. Otherwise, the beet root would pull all the water from the leaves. The pressure in the garden beet itself, according to the determination on September 28, was 11.81 atmospheres while in the leaves it was only 8.83. These pressures are comparable to those obtained by Pringsheim (14, page 135) for beets growing in damp soil, namely 11.68 atmospheres. The leaves were found by the same investigator to maintain a pressure of 15.52 atmospheres while still young, but with the growth of the leaf the pressure fell to 5.30 atmospheres, at which point it remained constant. The observations recorded in table 1 on October 1 for sugar beets and sugar beet leaves are even more divergent in their differences. The beets had a pressure of 17.18 atmospheres, while in one case the outer leaves had 9.65 and the inner, 11.42 atmospheres. All the leaves taken together from another beet plant gave 12.21 atmospheres. The soil water in the tracheae supplying the leaves from the fine rootlets must be practically impermeable to the high osmotic pressures surrounding them. Some water might be lost inward from one leaf cell to the adjacent ones nearer the stalk in the potato plant when the stalk has such a preponderance in osmotic pressure over that of the leaf, this process adding to the loss outward from transpiration. The total amount withdrawn by the cells may be small, but it may be the small excess that is necessary for the preservation

of turgor in these peripheral leaf cells. The bean and the corn plants were found to have a higher osmotic pressure in the stalks, and these plants do not often suffer from wilting of the tips and margins of the leaflets (with the resultant tip-burn) as do those of the potato plant. Several reasons may be given for this difference. The bean leaves in intense sunlight assume such a position that their laminae are parallel to the eight rays while the corn leaves roll up in intense heat. Neither of these plants is as succulent as the potato; the loss of water between adjacent cells ought to be very small as compared with that between the potato cells. The real cause for tip-burn in the potato may lie, too, in the movement of the elaborated food materials.

3. A high osmotic pressure does not seem to be necessary for the growth of reproductive organs nor for the continued deposition in them of reserve carbohydrates, such as starch or sugar. The sugar beet or the garden beet ought to be able to withdraw elaborated food materials from the leaves by osmotic pressure since their pressure is greater than that of the leaves. If these materials were put into the proper channels, they ought to find their way by osmosis to the storage organ. The continued growth of the potato tuber continues, however, when its osmotic pressure is only between 6 and 9 atmospheres, and at no time is the pressure greater in the tuber than it is in the leaves. The stalks record even a greater pressure than do the leaves. The movement of food materials is undoubtedly due to differences in osmotic pressures, but the manner in which they work to induce the flow of carbohydrates to the tubers is, as yet, unexplained.

The stalk of the plant seems to serve as an organ for temporary storage if the amount of sugar in it during periods of active carbon assimilation is an indication. Elaboration processes probably occur here but their nature is almost entirely speculation. The further translocation in the potato plant is dependent on the age of the plant; early in its growth, the material is used for the production of new leaves, but after the formation of the young tubers, the current changes its direction and the materials flow into them. The translocation of these carbohydrates probably occurs largely through the sieve-tubes according to the plant physiologists who have studied this phase of the subject; see Pfeffer (13, pp. 575–583) and Haberlandt (8, pp. 328–336). Neither of these authors, however, explains on the basis of experimental evidence the means by which the carbohydrate compounds are moved. Haberlandt (p. 334) makes the following statement concerning protein compounds: "When a petiole or stem of Cucurbita is cut across, large quantities of slimy protein-material exude from the several sieve-tubes. With reference to this point, A. Fischer has proved that the effects of a cut petiole extend through one or two internodes at the very least. This observation indicates that the pressure in the sieve-tubes is sufficient to overcome the resistance opposed by a very considerable number of sieve-plates. Thence we may infer that any differences which arise within the

intact sieve-tube system, owing to the partial depletion of the tubes at certain points, are at once equalized by a more or less rapid displacement of the liquid contents in the corresponding direction. Whether the hydrostatic pressure in the sieve-tubes owes its origin to the osmotic properties of the liquid contents or whether it is due to compression of the sieve-tubes by the highly turgescent adjoining tissues (leptome-parenchyma and companion cells) is still uncertain. Most probably both factors have a share in producing the pressure observed." He concludes: "This matter evidently requires further investigation."

The movement of food materials to the growing leaves of the young plant can be explained on the basis of high osmotic pressures in these organs, but the growth of the potato berries, of the young tomatoes, and of the potato tubers cannot be accounted for in any such manner since the osmotic pressure in all of these organs is the least of any in the plant. We must fall back upon the pumping action of the sieve-tubes as suggested by Haberlandt.

One question more remains to be answered: Why does the potato plant suffer from tip-burn while the tomato is usually exempt? This may be due to structural differences in the leaves or to the resistance of the cells to incipient wilting, but it seems to be better explained by the continued movement of the elaborated carbohydrates upward in the tomato plant to form new foliage while in the potato they travel downward to form starch in the tubers. The tomato leaves may be better nourished from this food stream, and the continued formation of vigorous new leaves helps, too, to shade the older ones that are more susceptible to abnormal evaporation.

Summary

1. The potato plant early in the season records the highest osmotic pressure in the sap from the young stalks and leaves.

2. During the very hot weather of July and August, the sap of the stalks develops a higher osmotic pressure than that from the younger portions of the plant.

3. The high pressure in the stalks is due to the presence in them of sugars, especially of cane sugar.

4. In September, after growth has been resumed, the young leaves again have the highest osmotic pressure of any portion of the plant.

5. The osmotic pressure of the sap of the growing tubers is always low and is intermediate between that of the sap of the stalk and the sap of the roots, which latter is the lowest of all.

6. The osmotic pressure in the older plants is higher than that in the younger ones and is due to the larger amounts of inorganic salts in the former. In very old plants, however, the soluble materials are removed to a considerable extent, and the osmotic pressure of the sap drops as a consequence.

VERMONT AGRICULTURAL EXPERIMENT STATION.

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